Annals
of the
Missouri Botanical Garden

Vol. 40 SEPTEMBER, 1953 No. 3

SOME AMERICAN MEDULLOSAS[1]

HENRY N. ANDREWS AND SERGIUS H. MAMAY[2]

The continued discovery of new species of the polystelic stems referable to the genus *Medullosa* emphasizes the conspicuous role that these plants played in the Pennsylvanian floras of the United States. Almost every large collection of coal balls that is studied reveals a specimen or two that differs in some way from those previously described. Although it has been impossible to define species limits with definite clarity when the specimens are fragmentary, poorly preserved, or represent only a short segment of the stem, it seems more than likely that most recorded American species are valid.

Those of us who have worked with these plants assumed some time ago that as the sources of material were more extensively explored our efforts would tend toward working out fine details rather than reporting ever more bizarre forms. Actually the reverse has proved to be the case, and the occurrence in recent collections of specimens of greater stem length has permitted more satisfactory study of variable characters such as stelar number.

One of the most notable contributions to our knowledge of the Medullosas is the recent description of *M. heterostelica* by Stewart and Delevoryas (1952). Although it is a bi-stelar stem the two steles divide in the nodal region to form a complex of twenty or more, some of which contribute to the petiole traces, whereas others reunite, the stem becoming bi-stelar again above the node. Had this specimen been found in a more fragmentary condition, descriptions of several "species" might well have resulted. As it is, the evidence suggests that stelar number is a reliable taxonomic character provided that a representative specimen of the stem is available.

The present account deals with several *Medullosa* specimens that have come to light in the paleobotanical laboratory of Washington University since Baxter's contribution in 1949. Certain of these add to our knowledge of the distribution of previously described species; others are distinctly new and present what we

[1] Publication authorized by the Director, U. S. Geological Survey.
[2] U. S. Geological Survey, Washington 25, D. C.

Issued September 30, 1953.

believe to be highly significant information bearing on the problem of the taxonomic significance of stelar number.

MEDULLOSA THOMPSONII Andrews

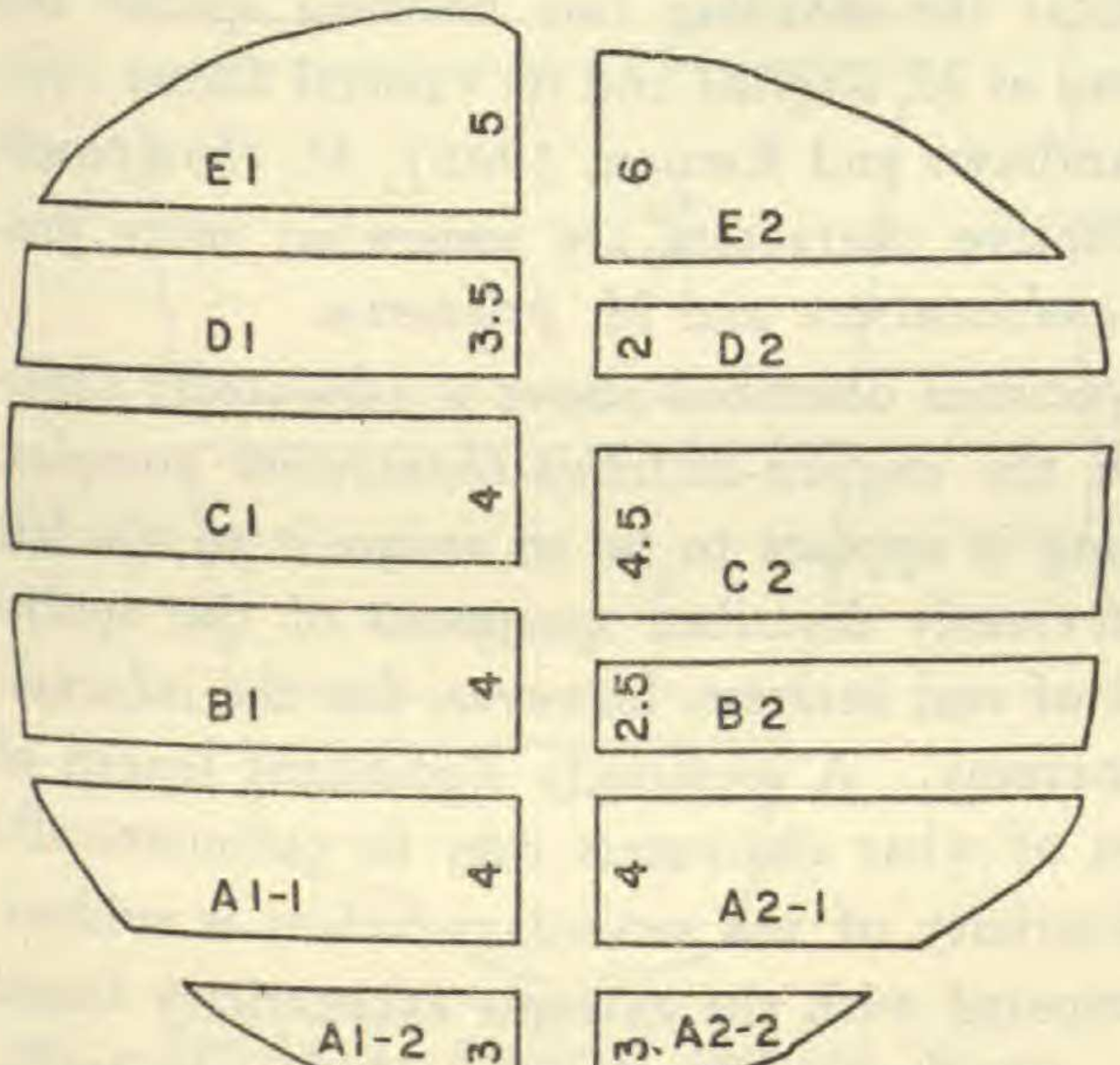
Two specimens referable to this species are present in our collections; both come from southeastern Kansas. One (No. 721) presents three steles (fig. 2), measuring 5 × 2.5 mm., 6 × 2.5 mm., and 2 mm. in diameter respectively and compares closely with the type specimen described from Iowa (Andrews, 1945). The second specimen is of interest because of its length and the type of stelar changes that occur. This stem, found in coal ball No. 713, is approximately 23 cm. long. No recognizable plant remains were evident on the exterior of the coal ball to guide the initial cut, and by chance the stem was dissected in a nearly median longitudinal plane. This seemed unfortunate at first, although it has materially aided us in following the changing stelar morphology through the length of the specimen. The plane of this initial cut accounts for the conspicuous break in certain of the cross-section illustrations (figs. 5-7).

Text-figures 1 and 2 show, respectively, a profile of the coal ball and a sketch of the stelar system indicating the divisions and fusions that take place. In the A1-2 and A2-2 blocks three steles (fig. 6) are present. These are enclosed by a clearly defined internal periderm that does not exceed 0.5 mm. in width and consists of rather thin-walled nearly cubical cells that present essentially the same appearance in transverse and radial sections. The steles at this point measure 13 × 9.5 mm., 11.5 × 6 mm., and 20 × 7 mm. In passing through the A1-1 and A2-1 blocks two of the steles fuse; the resultant two steles (fig. 7) measure 14 × 7.3 and 21.5 × 8 mm. Further divisions and fusions are indicated in text-fig. 2 as follows: In passing through the B blocks a stele divides, revealing three steles on the upper surface; in passing through the C blocks a fusion takes place, revealing two steles on the lower surface of D1 and D2; finally a small stele separates from one of the two steles, revealing three steles on the lower surface of the E blocks. Although the phloem is partly preserved, all stelar dimensions refer to the wood only.

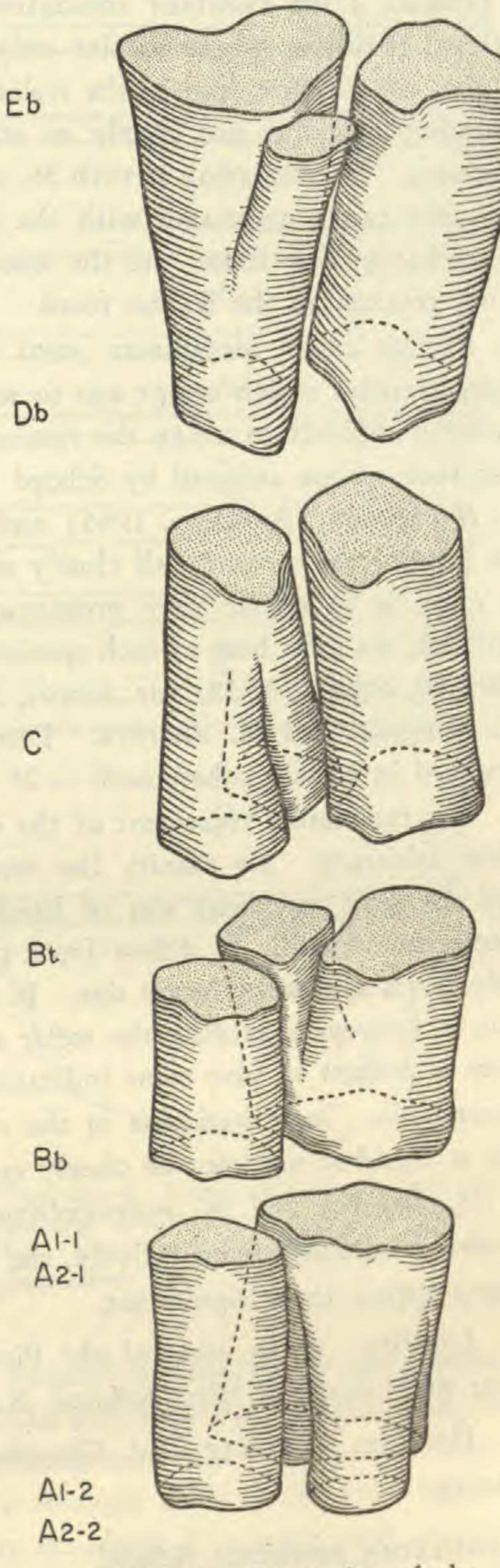
The secretory canals, which average about 0.3 mm. in diameter, are confined chiefly to the fiber zone of the cortex.

The primary body (fig. 3) contained a considerable amount of parenchyma, although this has decayed for the most part, leaving only the primary tracheids. The departing primary petiole strands are large and accompanied by little or no secondary wood. Through the length of this specimen there are at least two petioles that depart from the stem. It is especially important to note this, since obviously the type of nodal anatomy here is quite in contrast with that described for *Medullosa heterostelica*. This point will be considered in further detail under the description of the specimen that we are assigning to *M. heterostelica*.

The affinities of this stem seem to lie closest to *Medullosa distelica, M. anglica*, and *M. thompsonii*, but particularly the last. It differs from *M. distelica* in that



Text.-fig. 1. Profile of coal ball No. 713 containing specimen of *Medullosa thompsonii.* Numbers indicate thickness of blocks in centimeters.



Text-fig. 2. Restoration of the stelar system of *Medullosa thompsonii* (No. 713). Letters refer to the approximate position in the profile (text-fig. 1).

it presents a less constant association of secretory canals and fiber strands; an internal periderm which attains only about one-third to one-fifth the thickness of that of *distelica*; and in the stelar system the endocentric development of the secondary wood is not nearly so strongly pronounced nor as constant in our specimen. In comparing it with *M. anglica* it also appears to possess less abundant secretory canals associated with the fiber strands (Scott, 1899, pl. 12, fig. 14), somewhat smaller steles, and the secondary wood around the departing leaf traces is not retained in the Kansas fossil.

Almost every Medullosan stem discovered in American coal balls displays characteristics which tempt one to set up a new specific entity, or which at least render it difficult to assign the specimen with confidence to an established species. The four species assigned by Schopf (1939) to his subgenus *anglorota* as well as *M. thompsonii* (Andrews, 1945) and the species described more recently by Baxter (1949) are certainly all closely related. With some species the relationship is so close as to render very problematical the dividing line between species and varieties; we refer here to such specimens as *M. anglica* and its varietal forms (var. *thiesseni*, Schopf, 1939; var. *ioensis*, Andrews and Kernen, 1946), *M. thompsonii*, *M. elongata*, and *M. distelica*. Distinctive characters are somewhat more pronounced in certain others such as *M. endocentrica* and *M. primaeva*.

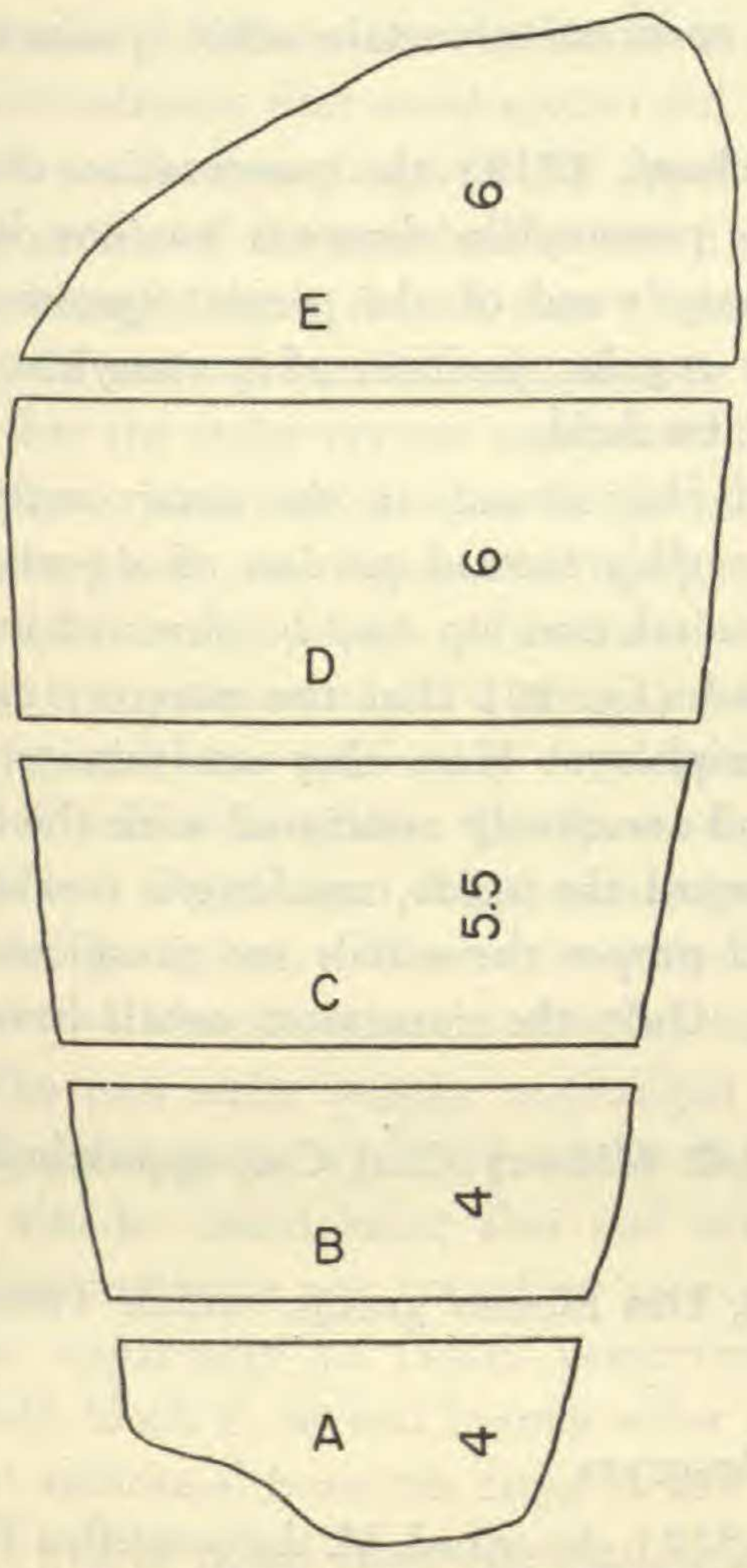
The taxonomic treatment of the specimen described above is admittedly somewhat arbitrary. Its affinity lies with the *anglica-distelica-thompsonii* complex, and the most expedient way of handling it appears to be to assign it to the last species mentioned. It differs from previously described specimens of this species only in its somewhat larger size. It is of real interest, however, for the information it conveys regarding the stelar anatomy. A seemingly significant length of stem is present to give some indication of what characters may be taxonomically dependable. Some variation in the centricity of the secondary xylem is evident, but it could at no point be closely compared with the extreme excentricity found in *M. distelica* and *M. endocentrica*. Within certain limits, which admittedly cannot be defined quantitatively, the degree and form of excentricity in *Medullosa* stems appear to be significant.

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

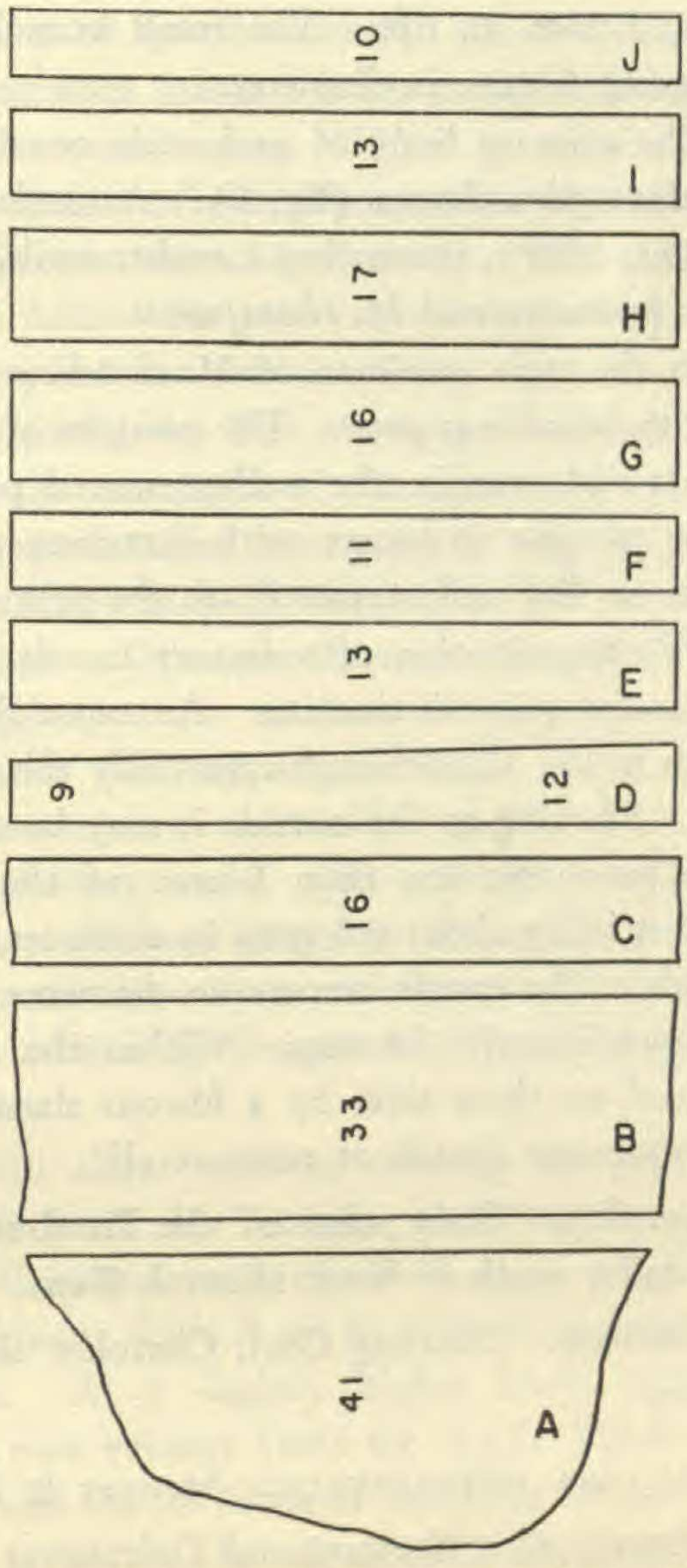
Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

Medullosa distelica Schopf

Another *Medullosa* specimen (No. 688) from the West Mineral, Kans., locality appears to be referable to this two-stelar species described by Schopf (1939) from the No. 6 coal of Illinois. It is basically a two-stelar specimen but presents certain variations which seem significant in furthering our knowledge of what may be considered to be specific boundaries in the genus.



Text-fig. 3. Profile of coal ball No. 688 containing specimen of *Medullosa distelica.* Numbers indicate thickness of the blocks in centimeters.



Text-fig. 4. Profile of coal ball No. 819 containing specimen of *Medullosa heterostelica.* Numbers indicate thickness of blocks in millimeters.

It has been possible to follow the stem through a distance of approximately 10 cm. (text-fig. 3). The stelar system and the enclosing periderm are quite well preserved, but the cortical tissues have been distorted and a considerable amount lost. In block *A* the stem is composed of two strongly endocentric steles (fig. 4). In the stem's course through the lower part of block *B* a small stele separates from one of the original two, producing a three-stelar system. After another 4 cm. the two-stelar phase is resumed, but since the preservation is poor beyond this point it has not been possible to determine whether any other changes take place.

The two principal steles measure about 18 × 6 mm. and 14 × 5 mm.; taking into account the obvious crushing, they measured approximately 18 × 8 mm. and

14×7 mm. in life. The small branch stele is nearly round in cross-section, measuring 5 mm. in diameter.

The primary body of each stele consists of scattered groups of tracheids and abundant parenchyma (fig. 9). A similar ratio occurs in *Medullosa endocentrica* (Baxter, 1949), presenting a rather striking contrast to certain other species such as *M. primaeva* and *M. thompsonii.*

In the type specimen of *M. distelica* (Schopf, 1939) the preservation of the primary wood was poor. The position of the protoxylem elements was not determined; and even in the well-preserved primary wood of the present specimen it is not possible to locate with certainty any regular position of protoxylem elements, so few and scattered are the primary tracheids.

The organization of secretory canals and fiber strands in the outer cortex or rind seems quite distinctive. An especially well-preserved portion of a petiole is shown in fig. 17, although essentially the same relationship may be observed in the stem. Starting at the outside it may be noted (fig. 10) that the secretory canals reach to within less than 1 mm. of the periphery. Here they are minute, the smallest being about 0.1 mm. in diameter, and are closely associated with the fiber strands. The canals increase in diameter toward the inside, reaching a maximum of approximately 2.5 mm. Within the rind proper the canals are conspicuously enclosed on three sides by a fibrous sheath. Only the outermost canals have an inconspicuous sheath or none at all.

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

MEDULLOSA HETEROSTELICA Stewart & Delevoryas

Shortly after Stewart and Delevoryas (1952) described *M. heterostelica* from West Mineral, Kans., the present writers collected from the same locality a coal ball (No. 819) containing a stem which displays strikingly similar gross morphology. The stem has two steles which divide into more than fourteen, presumably in the nodal region. It differs from the type specimen, however, in two ways:

1. The two original steles in No. 819 measure about 16 mm. in diameter (xylem only) and are radially symmetrical with reference to both primary and secondary wood. The steles of the type specimen measure 5×8 mm., being less than one-half the diameter of those in our specimen.

2. The over-all size and form comparison is also reflected in the primary wood. The ratio of tracheids and parenchyma in the primary wood of the two seems to be comparable; but in No. 819 the size of the tracheids is conspicuously greater, and the primary body is nearly circular, whereas that of the type specimen is elongate.

A wholly satisfactory comparison of the two is impossible since the cortical tissues and leaf bases of our specimen are not preserved. It is, therefore, only on the characters cited above that a decision as to specific identity can be made.

The chief point of interest that the specimen presents is the remarkable multiplication of steles in what we assume is the nodal region. This is in notable contrast to the stelar anatomy of any other species of *Medullosa,* and it is of course important to determine whether it is a specific character in itself. The evidence to date indicates that some species did not follow this pattern, whereas with others (based on short or fragmentary specimens) we cannot be certain.

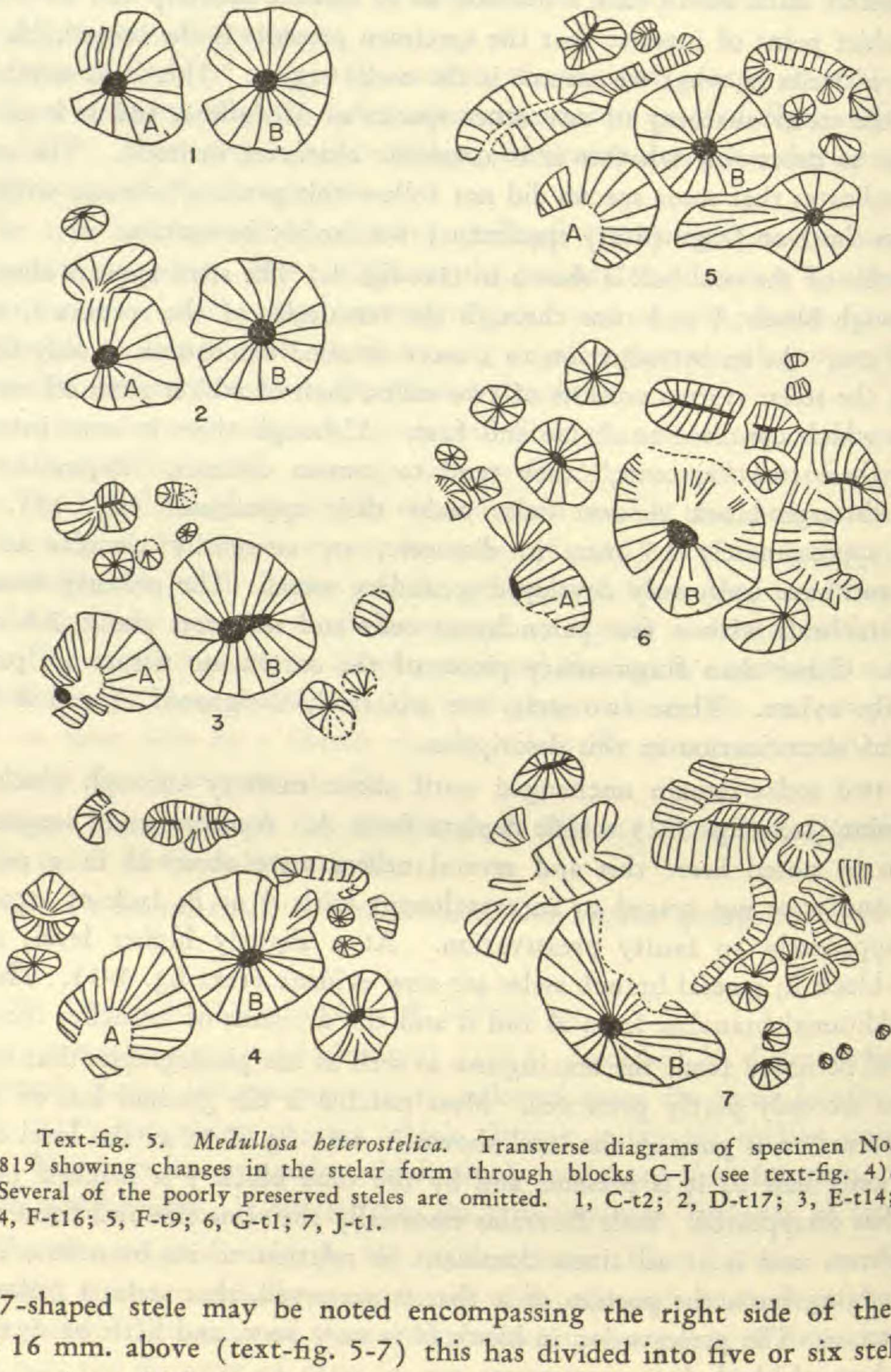
A profile of the coal ball is shown in text-fig. 4. The stem appears about midway through block *A* and runs through the remainder of the specimen, totaling about 15 cm. As an introduction to a more detailed description it may be noted first that the stelar system consists of two steles, each of which gives off numerous branches which continue to divide and fuse. Although there is some interfusion between these two "systems," they tend to remain distinct. Beginning about midway through block *A* two steles make their appearance (fig. 11). They measure approximately 16 mm. in diameter, are essentially circular in cross-section, and have uniformly developed secondary wood. The primary wood consists of tracheids with a few parenchyma cells and measures about 2.5 mm. in diameter. Other than fragmentary pieces of the cortex, no tissues are preserved outside the xylem. These two steles are arbitrarily designated *A* and *B* for the purpose of identification in this description.

The two steles remain unchanged until about midway through block *D,* at which point (text fig. 5-2) a stele departs from *A.* Another small separate stele may also be noted here; this and several others were observed in a peripheral position and were not traced to an attachment with *A* or *B*; lack of attachment is due apparently to faulty preservation. At a slightly higher level, midway through block *E,* several branch steles are now evident (text fig. 5-3). These represent additional branches from *A* and *B* and the divisions of branches themselves.

It will be noted from the text figures as well as the photographs that many of the steles are only partly preserved. Most notable is the gradual loss of stele *A.* The preservation is poor at the level shown in text-fig. 5-3; at the level of text-fig. 5-5 only half of it is present, and by the time block *J* is reached (text-fig. 5-7) it has disappeared. Stele *B* retains essentially the same size and form through the specimen and is at all times dominant in relation to its branches; it seems likely, judging from the portion of it that is preserved, that stele *A* followed the same pattern. The preservation in block *H* is very poor, and little of significance remains beyond block *J.*

For the most part, the branch steles shown on the left side of the text-figures come from stele *A* and those on the right side from stele *B.* A union of the two "systems," however, is evident in text-fig. 5-6 in the form of the elongate stele in the upper part of the figure.

The maximum number of steles present at any one point can be determined only approximately, because of faulty preservation and in part because of the prolific anastomosing nature of the system. For example, in text-fig. 5-6 a more



Text-fig. 5. *Medullosa heterostelica.* Transverse diagrams of specimen No. 819 showing changes in the stelar form through blocks C–J (see text-fig. 4). Several of the poorly preserved steles are omitted. 1, C-t2; 2, D-t17; 3, E-t14; 4, F-t16; 5, F-t9; 6, G-t1; 7, J-t1.

or less 7-shaped stele may be noted encompassing the right side of the figure, whereas 16 mm. above (text-fig. 5-7) this has divided into five or six steles. At the latter point, which may be taken as representative of the more highly divided part of the stem, there are about fourteen whole or fragmentary steles.

So poorly is the stem preserved beyond block *J* that we are unable to determine whether or not it passes back into the two-stelar phase as reported for the type specimen. The lack of cortical tissues and petiole bases also makes it impossible to determine which steles contribute directly or indirectly to the petiole trace system.

The only previously described *Medullosa* specimen with which this may be compared closely is *M. heterostelica.* As stated above, it differs most notably in size, the two central steles being twice as great in diameter as those of the type specimen. Assuming that the multiple stelar condition in our specimen is also a nodal region, the size contrast is comparable here. This region is described as being approximately 5.5 cm. long in the type specimen (Stewart and Delevoryas, 1952, p. 508, figs. 5 and 12). In our specimen the multiple-stelar phase starts in block *D* and runs through *J*, a distance of 9.3 cm., and undoubtedly ran for several centimeters more if indeed it did again assume the two-stelar phase.

Aside from the size there is nothing on which to base a specific difference, and for that reason our specimen is assigned to *M. heterostelica.*

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

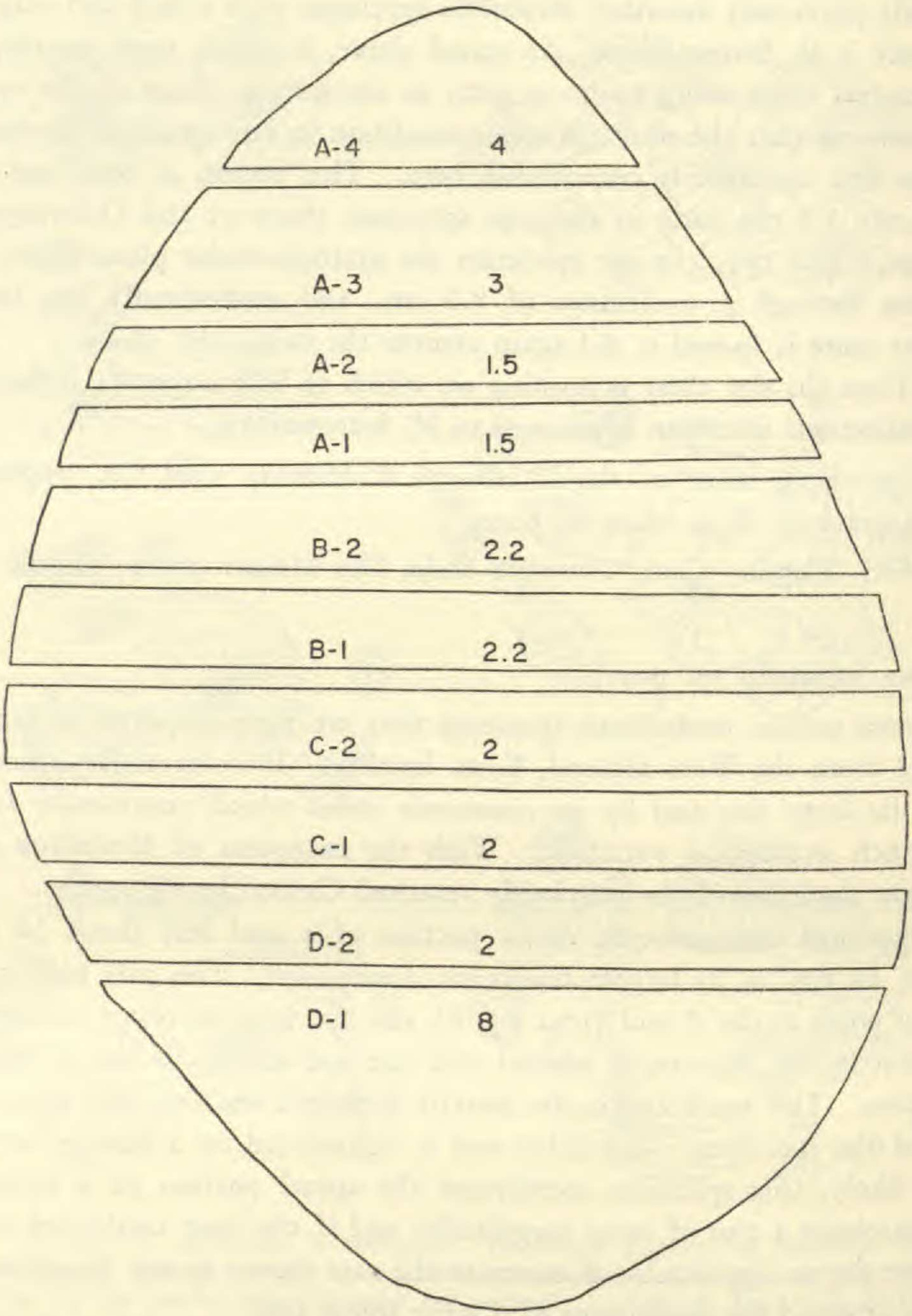
MEDULLOSA **grandis** sp. nov.

The most unique medullosan specimen that we have acquired in recent years is No. 718 from the West Mineral, Kans. locality. It is especially interesting by virtue of its large size and by its numerous steles which anastomose freely and present much anatomical variation. With the exception of *Medullosa noei* it is much larger than any of the previously reported Carboniferous species.

The specimen composes the major portion of a coal ball about 30 cm. long and 28 × 12 cm. in its largest transverse dimensions. The coal ball tapers to a very blunt point at the *A* end (text-fig. 6) and the stem decreases correspondingly in size; that is, the decrease is normal and not due simply to loss of part of the stelar system. This small end is also heavily pyritized and less well preserved than the rest of the specimen. The other end is represented by a broken surface. If, as seems likely, this specimen constitutes the apical portion of a stem, then it clearly represents a tree of some magnitude; and if the stem continued to increase in diameter for an appreciable distance at the rate shown in our fragment it must have soon attained the dimensions of a large forest tree.

In order to present a clear picture of the complex organization of the stelar system a restoration of the major portion of it is shown in text-fig. 7. This is accompanied, in text-fig. 8, with diagrams of the system at the four points indicated. All the numerous smaller steles that show in text-fig. 8 are not included in the restoration (text-fig. 7). Text-fig. 6 is a profile of the coal ball, which may be referred to for the position of the text and plate figures.

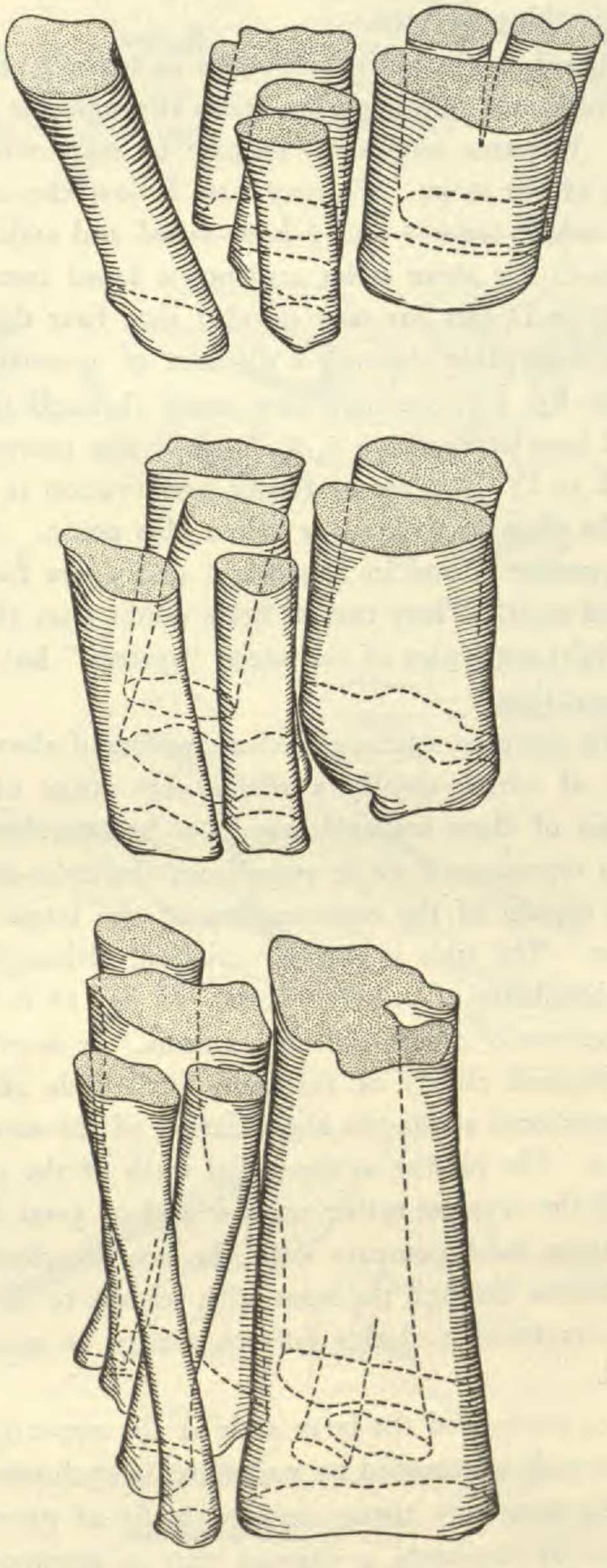
A casual glance at the text-figures reveals considerable variation in the size and shape of the steles as well as the relative amount of primary wood that is present. A striking feature is the great variation in the structure of the secondary wood itself, in which the different ratios of parenchyma and tracheids present distinctly atypical steles. It is of course likely that many of the smaller strands



Text-fig. 6. Profile of coal ball No. 718 containing the specimen of *M. grandis.* Numbers in the right column indicate thickness in centimeters.

contribute to the vascular supply of the petioles. Of necessity we are therefore using the term "stele" to include all the vascular strands with secondary wood (secondary phloem is present but poorly preserved).

In tracing the over-all pattern of the stelar anatomy it is significant to note that it is composed of two fairly distinct systems, thus following in a general way the type of organization described for *Medullosa heterostelica.* Stelar branching and fusion take place so rapidly that the system presents an intricate anastomosing network. The block is so large that it did not seem practicable to run a complete



Text-fig. 7. A restoration of the stelar system of *Medullosa grandis*.

series of sections through the specimen. Text-fig. 7 presents, therefore, a slightly less complex picture than that actually represented by the number of steles involved and the branching pattern.

The numbers assigned to the individual steles in text-fig. 8 *A–D* are arbitrary and are intended to facilitate following the steles through the portion of the stem that is represented. It seems somewhat simpler to start with the smaller end, presumably the apex of the stem. We may first follow the course of steles 1, 2, and 3 from *A* to *B*, where steles 1 and 2 have fused and stele 3 is evidently preparing to divide. In *C* the three steles are shown fused into a single irregular-shaped stele. Finally in *D* this has now divided into four distinct steles. These fusions and divisions take place through a distance of approximately 10 cm.

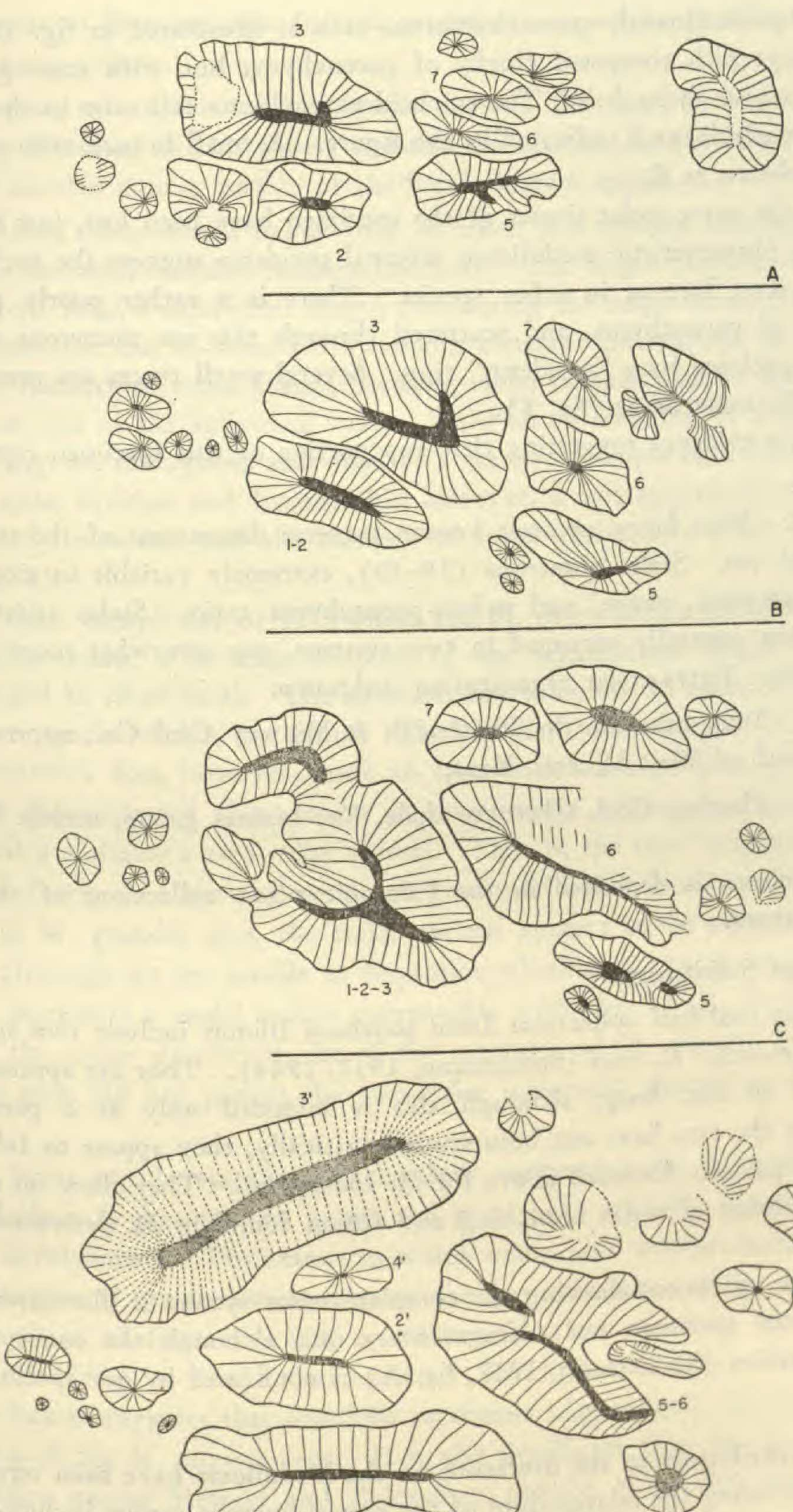
Returning to text-fig. 8-*A* we may now trace through the second "system" of steles, represented here by numbers 5, 6, 7; these also increase markedly in size in passing through *B* to *C*. Because of faulty preservation it was not possible to interpret precisely the changes that ensue below this point. At least one branch stele departs from number 5, and in *D* steles 5 and 6 are fused to form a very irregular-shaped wood mass. There can be little doubt that the numerous smaller steles shown to the right are a part of this stelar "system," but they have not been traced in actual connection.

In addition to the more conspicuous steles considered above there are numerous smaller ones all of which display a remarkable range of variation in their organization. Certain of these features may now be considered.

Figure 13, which represents a single stele from the cross-section shown in fig. 1, may be taken as typical of the organization of the larger "normal" vascular elements of the stem. The stele is slightly crushed, although it is evident that there was no great abundance of primary wood. In fig. 14 is illustrated a portion of another stele of generally comparable dimensions. It is evident here that the primary wood is composed chiefly of tracheids with little admixed parenchyma. There is nothing exceptional about the organization of the secondary wood of the stele shown in fig. 13. The pitting in the radial walls of the tracheids is typically pteridospermous, and the rays are rather narrow and of great height.

Several of the larger steles compare with the one described above, but others vary much in their course through the stem with respect to the relative abundance of parenchyma and tracheids, and this difference may be noted in both primary and secondary wood.

Figure 16 shows a portion of the large stele at the upper right of fig. 1. The central region of this stele is occupied by parenchyma exclusively, whereas the immediately surrounding secondary tissue consists chiefly of parenchyma with a few radially aligned rows of tracheids, a feature that is common in the secondary xylem of some of the large Permian Medullosas. Toward the periphery of the stele the organization compares closely with that observed in the stele shown in fig. 13. It should be kept in mind here that the stele shown in fig. 16 is directly connected with the "normal" stele shown in fig. 13.



Text-fig. 8. *Medullosa grandis.* Transverse diagrams of specimen 718 showing changes in the stelar form through blocks A–C (See text-fig. 6). A, A-t2; B, B2-t1; C, B1-t1; D, C-t1.

Another predominantly parenchymatous stele is illustrated in fig. 15. Here there is a large pith composed chiefly of parenchyma but with some groups of tracheids scattered through it. The tracheid-parenchyma cell ratio in the secondary wood is variable, as is indicated in the figure. A small branch stele preparing to depart is shown at *B*.

Most of the extra-stelar tissues of the specimen have been lost, but the fragments of the characteristic medullosan internal periderm suggest the enclosure of the stelar system here as in other species. There is a rather poorly preserved groundwork of parenchyma, and scattered through this are numerous secretory canals, each enclosed by a "periderm" ring. Several small traces are present, also enclosed in the same tissue (fig. 8).

There is no evidence suggesting that any portion of this specimen represents a nodal region.

Diagnosis: Stem large, greatest known traverse dimensions of the stelar system 12 × 28 cm. Steles numerous (18–20), extremely variable in size (up to 6 cm. in diameter), shape, and xylem-parenchyma ratio. Steles anastomosing frequently, but generally arranged in two systems, one somewhat more complex than the other. Extra-stelar organization unknown.

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

Type specimen is deposited in the Paleozoic plant collections of the U. S. National Museum.

Medullosa noei Steidtmann

Our recent coal-ball collections from southern Illinois include two specimens of the large tri-stelar *M. noei* (Steidtmann, 1937, 1944). They are approximately 43 cm. and 30 cm. long; although this is intended only as a preliminary account, since the two have not been studied critically, they appear to follow the general stelar pattern described above for *M. thompsonii*. They show no evidence of the multiplicity of stelar branching and fusion found in *M. heterostelica* and *M. grandis*.

One of the specimens showing the complete stelar system is illustrated in fig. 18; the original specimen was a fragmentary one, although the concept of its stelar organization (Steidtmann, 1937, fig. A) is confirmed by our specimens.

Discussion:

Several contributors to the literature on the Medullosas have been tempted to speculate concerning the relationships of the now numerous species included in the genus. A total of no less than 44 species and varieties have been recorded to date, and since the stelar anatomy is nearly as diverse as the number of entities recorded it is understandable that paleobotanists find it intriguing to propose evolutionary lines in the group. Although the primary purpose of this paper is to present what appear to be significant factual contributions, a few speculatory comments seem to be in order.

One point of anatomical significance is well illustrated by the assemblage of specimens discussed in this paper, namely, the contrast in the relative constancy of stelar number among certain of the better-known species.

Medullosa endocentrica Baxter may be taken as a striking example of a species in which the stelar number remains constant. The single available specimen was some 12 cm. long, a significant length considering the small diameter of the plant. In this specimen the tri-stelar form remains constant throughout its length, there being no evidence of stelar fusion, division, nodal complexities, or notable changes in shape or size of the individual steles. Based on observations of a specimen some 23 cm. long, *M. thompsonii* also displays a relatively simple stelar pattern. There is some stelar division and fusion; this, however, is not apparently related to the position of the nodes, and the number of steles varies only from two to three (text-fig. 2).

The stelar complexity of *M. grandis* and *M. heterostelica* presents, at least on casual observation, a striking contrast to the organization found in *M. endocentrica* and *M. thompsonii.* The contrast may cause one to question the inclusion of all four species within one genus. The complex stelar form of *M. grandis* and *M. heterostelica* does, however, mask an apparently basic pattern of organization. We have demonstrated that, so far as preservation allows, our specimen of *M. heterostelica* contains a two-stelar system. That is, the two "original" steles each divide profusely, but the two resultant groups of steles remain more or less distinct. In *M. grandis*, also, the stelar system appears to be organized into two groups, although we are unable to determine whether or not the specimen at our disposal represents a nodal region comparable with that of *M. heterostelica.* In view of the rather significant size of the specimen of *M. grandis*, it seems likely that the stem did not possess the two-stelar internodal simplicity of *M. heterostelica.*

One point can be stated with certainty concerning the interrelationships of the Medullosas is that we can guess, and guess only vaguely, concerning possible lines of development. The extent to which competent workers have disagreed in their concepts of racial development in the genus is indicated by comparing the phyletic chart of Baxter (1949, p. 309) with that presented by Stewart and Delevoryas (1952, p. 514). In the latter, *Sutcliffia* is assigned a basal position, whereas Baxter suggests that *Sutcliffia* represents a specialized side branch from a *Medullosa* of the *M. anglica* type. It is also significant that the discovery of *M. heterostelica* caused Stewart and Delevoryas (1952) to modify rather radically the concept presented in Stewart's earlier paper of 1951.

It is thus evident that the discovery of each new species of *Medullosa* may result in a new phyletic scheme for the genus, particularly in view of the unique specimens that have been discovered in recent years. Our feeling is that interrelationships within the genus are actually much more complex than has been implied by previous workers. Evidence in support of this view is contributed by the recent report of *M. olseniae* from the Permian of Texas (Roberts and Barghoorn, 1952). It is a multi-stelar stem, the steles being arranged in a peripheral group resembling *M. leuckarti* or *M. solmsi*, but subsidiary steles are reported to be lacking. It is thus difficult to "fit" it into the top of either of the two branches of the genus indicated in the chart presented by Stewart and Delevoryas.

Although we shall refrain from commenting further on the evolution of the genus as a whole, we should like to conclude with a comment on the type of anatomy presented by the *grandis-heterostelica* complex. It has been assumed by many previous workers that the Medullosas evolved from a single-steled plant of the *Heterangium* type or one in which a single stele appears dominant, as in *Sutcliffia*. Referring for the moment to the type of anatomy exhibited by *M. grandis*, there appear to be at least two possible explanations for its origin:

First, in view of the two distinct stelar "systems" represented, *Medullosa grandis* may be considered as having evolved from a *two-stelar* ancestor with stelar proliferations resulting in this type of multi-stelar stem. Further modifications of the *M. grandis* pattern may then have resulted in the diverse types found in the Permian. Then, unless we assume a *phyletic return* to the two-stelar form, *M. grandis* may be considered as an advanced species having evolved from the *anglica-thompsonii-distelica*-etc. group. Stratigraphic relations are not very helpful here. The exact position of *M. grandis* in relation to the species cited above is not known, but it seems likely that *M. anglica* is of earlier origin, while *M. thompsonii* and *M. distelica* are of later origin (see Andrews, 1951, p. 433).

Second is the possibility that *M. grandis* is a distinctly *primitive Medullosa* in which we may see the beginnings of dominance being assumed by a few steles. In this case *M. heterostelica* may represent a species in which the multi-stelar phase is confined to the nodal region and in turn the two- to three-stelar species have evolved (as suggested by Stewart and Delevoryas) by the complete loss of the multi-stelar phase. This suggestion next requires some tentative explanation concerning the origin of *M. grandis*, and it is at this point that we would diverge most radically from previous views.

In recent years several poly-stelic plants have been reported from Devonian and lowermost Carboniferous horizons such as *Xenocladia* (Arnold, 1952), *Pietzschia* (Gothan, 1927; and Read and Campbell, 1939), *Steloxylon* (Solms-Laubach, 1896, and Read and Campbell, 1939), and *Cladoxylon* (Bertrand, 1935). It is not implied that *M. grandis* may be traced directly to any of these plants, but it is suggested that such a stem *type* may represent a medullosan ancestor.

Acknowledgement:

This study has been aided in large part by a grant from the Permanent Science Fund of The American Academy of Arts and Sciences. A portion of the work was also carried out during my tenure, at Harvard University, as a Fellow of the John Simon Guggenheim Memorial Foundation. I am sincerely grateful to these several institutions.—H.N.A.

References:

Andrews, H. N. (1945). Contributions to our knowledge of American Carboniferous Floras. VII. Some Pteridosperm stems from Iowa. Ann. Mo. Bot. Gard. 32:323–360.

———, (1951). American coal-ball floras. Bot. Rev. 17:430–469.

———, and Kernen, Jules A. (1946). Contributions of our knowledge of American Carboniferous Floras. VIII. Another Medullosa from Iowa. Ann. Mo. Bot. Gard. 33:141–146.

Arnold, C. A. (1952). Observations on fossil plants from the Devonian of eastern North America. VI. *Xenocladia medullosina* Arnold. Univ. Michigan, Contr. Mus. Paleont. 9:297–309.

Baxter, Robert W. (1949). Some Pteridosperm stems and fructifications with particular reference to the Medullosae. Ann. Mo. Bot. Gard. 36:287–352.

Bertrand, Paul (1935). Contribution à l'étude des Cladoxylées de Saalfeld. Palaeontographica 80B: 101–170.

Gothan, W. (1927). Strukturzeigende Pflanzen aus dem Oberdevon von Wildenfels. Abh. Sächs. geol. Landesanstalt 3:1–11.

Read, C. B., and Campbell, G. (1939). Preliminary account of the New Albany shale flora. Amer. Midl.Nat. 21:435–453.

Roberts, David C., and Elso S. Barghoorn (1952). *Medullosa olseniae*: a Permian *Medullosa* from north central Texas. Harvard Univ., Bot. Mus. Leafl. 15:191–200.

Schopf, J. M. (1939). *Medullosa distelica,* a new species of the *anglica* group of Medullosa. Amer. Jour. Bot. 26: 196–207.

Scott, D. H. (1899). On the structure and affinities of fossil plants from the Palaeozoic rocks. III. On *Medullosa anglica,* a new representative of the Cycadofilices. Roy. Soc. London, Philos. Trans. 191:81–125.

Solms-Laubach, H. (1896). Ueber die seinerzeit von Unger beschreibenen strukturbietenden Pflanzenreste des Unterculm von Saalfeld in Thüringen. Preuss. Geol. Landesanstalt Abh., neue Folge 23:1–100.

Steidtmann, Waldo E. (1937). A preliminary report on the anatomy and affinities of *Medullosa noei,* sp. nov. from the Pennsylvanian of Illinois. Amer. Jour. Bot. 24:124–125.

———, (1944). The anatomy and affinities of *Medullosa noei* Steidtmann, and associated foliage, roots, and seeds. Univ. Michigan, Contrib. Mus. Paleont. 6:131–166.

Stewart, Wilson N. (1951). *Medullosa pandurata* sp. nov. from the McLeansboro group of Illinois. Amer. Jour. Bot. 38:709–717.

———, and Delevoryas, Theodore (1952). Bases for determing relationships among the Medullosaceae. *Ibid.* 39:505–516.

Explanation of Plate

PLATE 16

Fig. 1. *Medullosa grandis* Andrews & Mamay. Transverse section, peel 718-C-tl. Natural size.

1.

ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

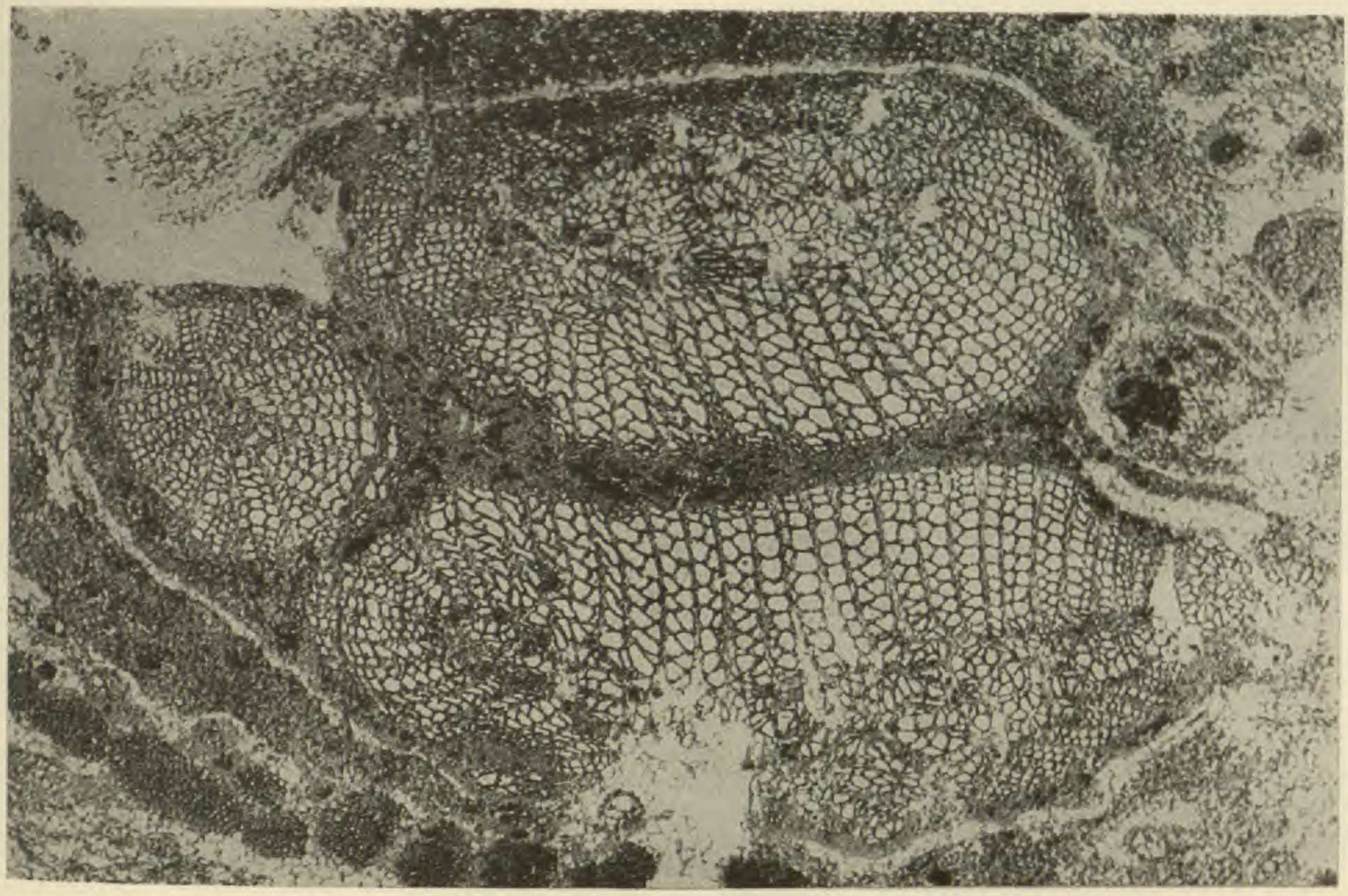
Explanation of Plate

PLATE 17

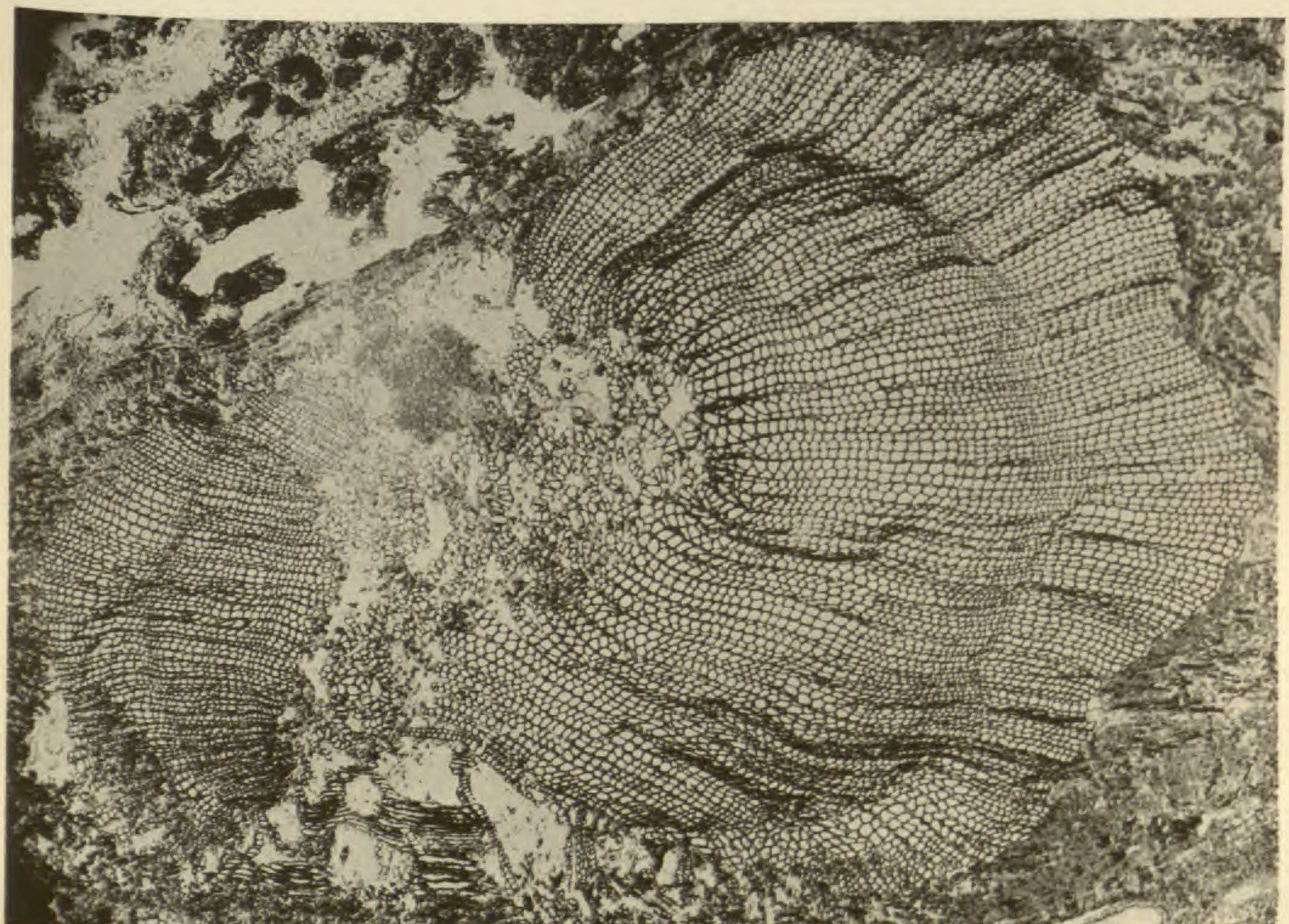
Medullosa thompsonii Andrews

Fig. 2. Transverse section of stelar system of specimen No. 721. Peel 721-B-b2. × 14.

Fig. 3. Transverse section of a single stele of specimen No. 713. Peel 713-D2-t4. × 8.

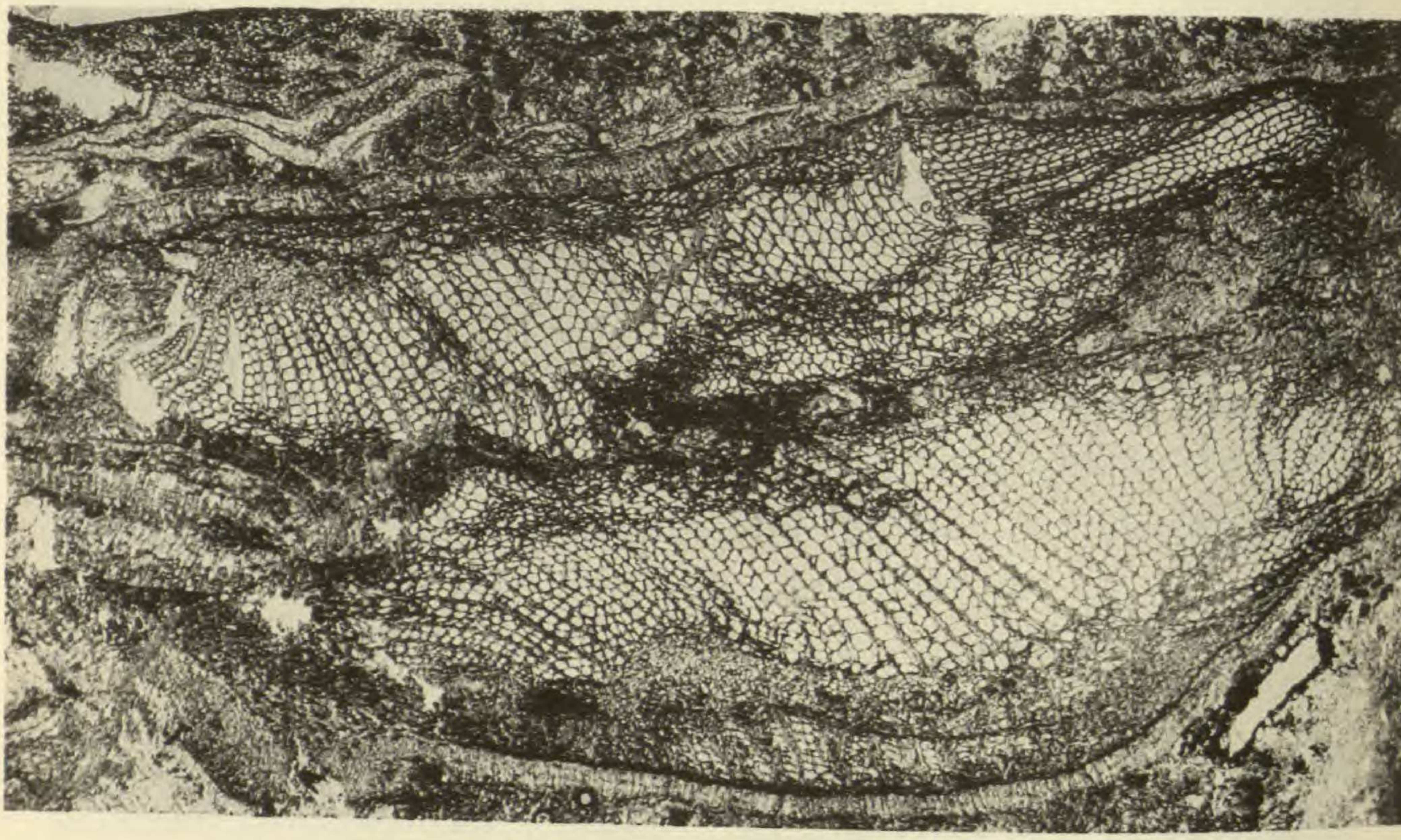


2



3

ANDREWS AND MAMAY — AMERICAN MEDULLOSAS



4

5

ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

Explanation of Plate

PLATE 18

Fig. 4. *Medullosa distelica* Schopf. Transverse section of stelar system of specimen No. 688. Peel 688-A-t13. × 15.

Fig. 5. *Medullosa thompsonii* Andrews. Transverse section of specimen No. 713 showing two-stelar phase. Peels 713-D2-b3 and 713-D1-b3. × 4.

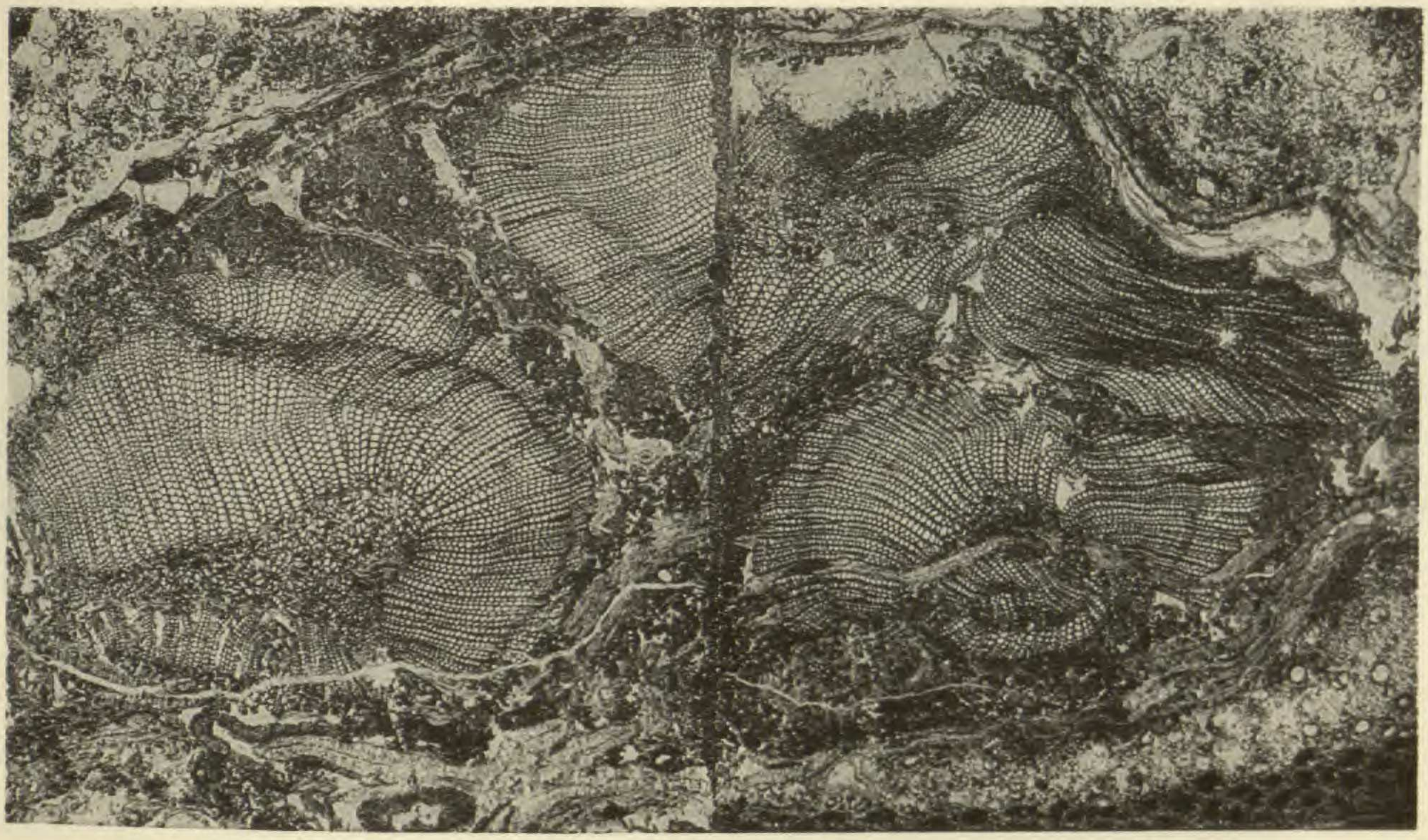
Explanation of Plate

PLATE 19

Medullosa thompsonii Andrews. Transverse sections of stelar system.

Fig. 6. Peels 713-A1-1,b2 and 713-A2-1,b2. × 4.

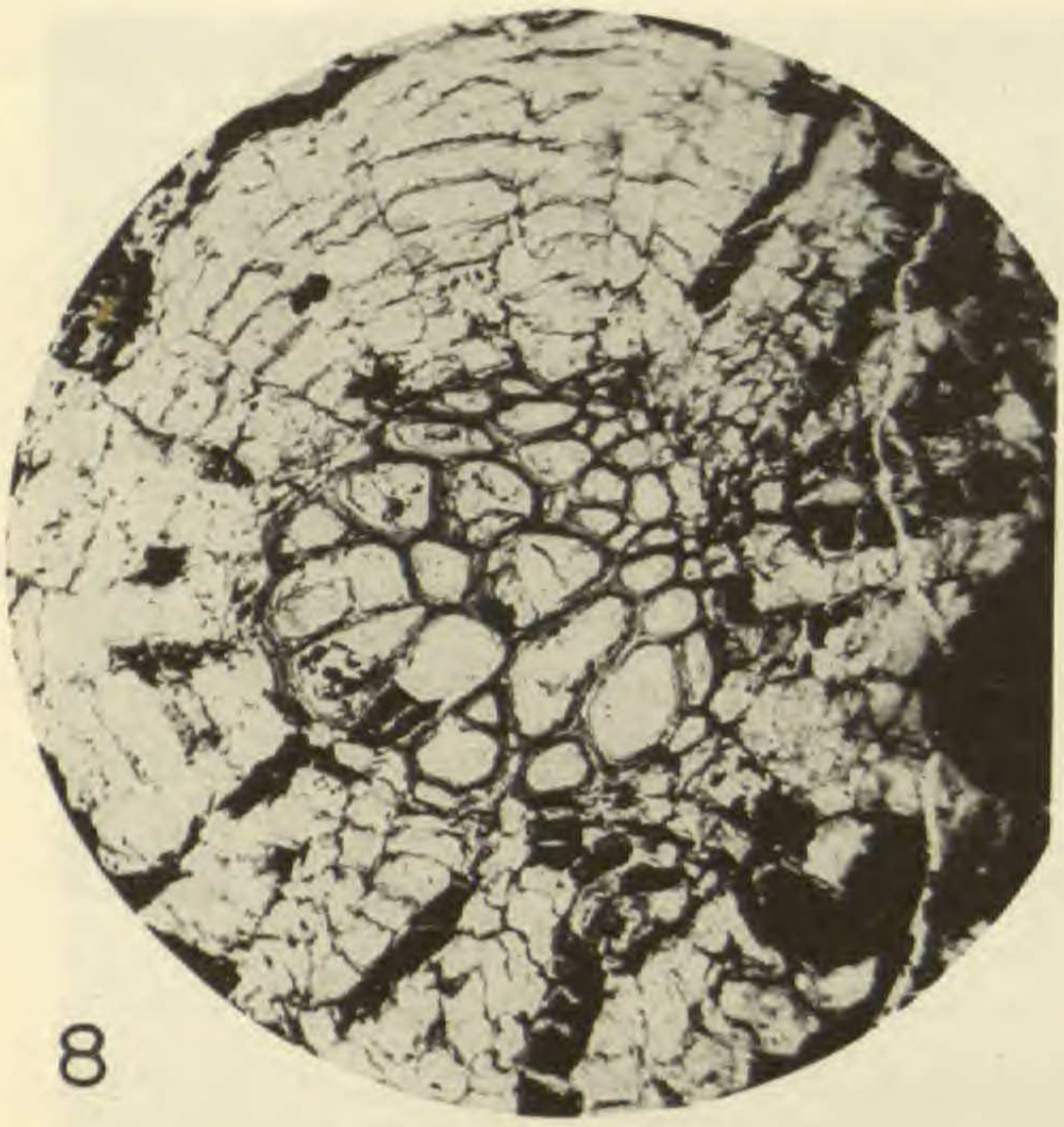
Fig. 7. Peels 713-B1-b7 and 713-B2-b8. × 4.



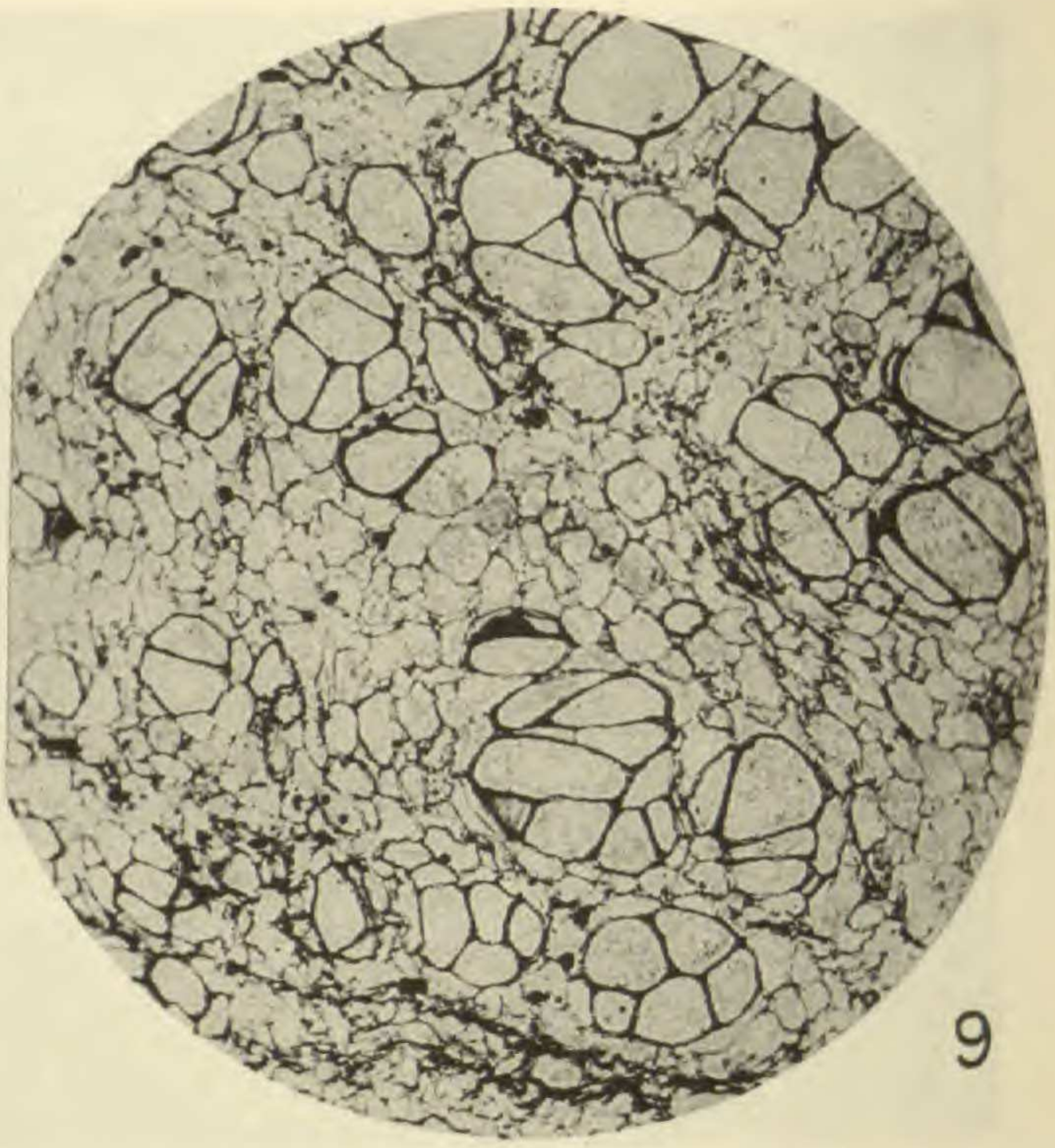
6

7

ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

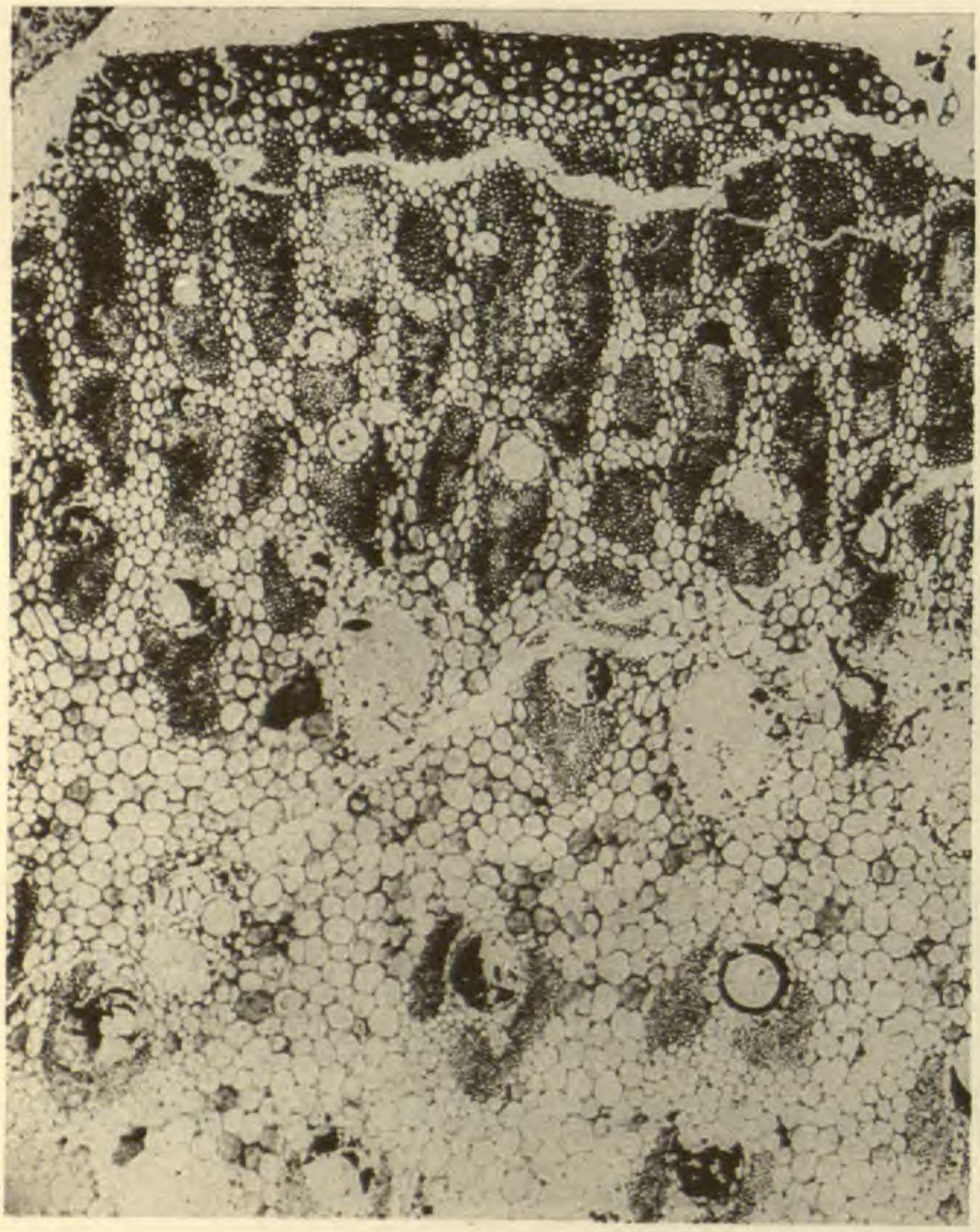


8

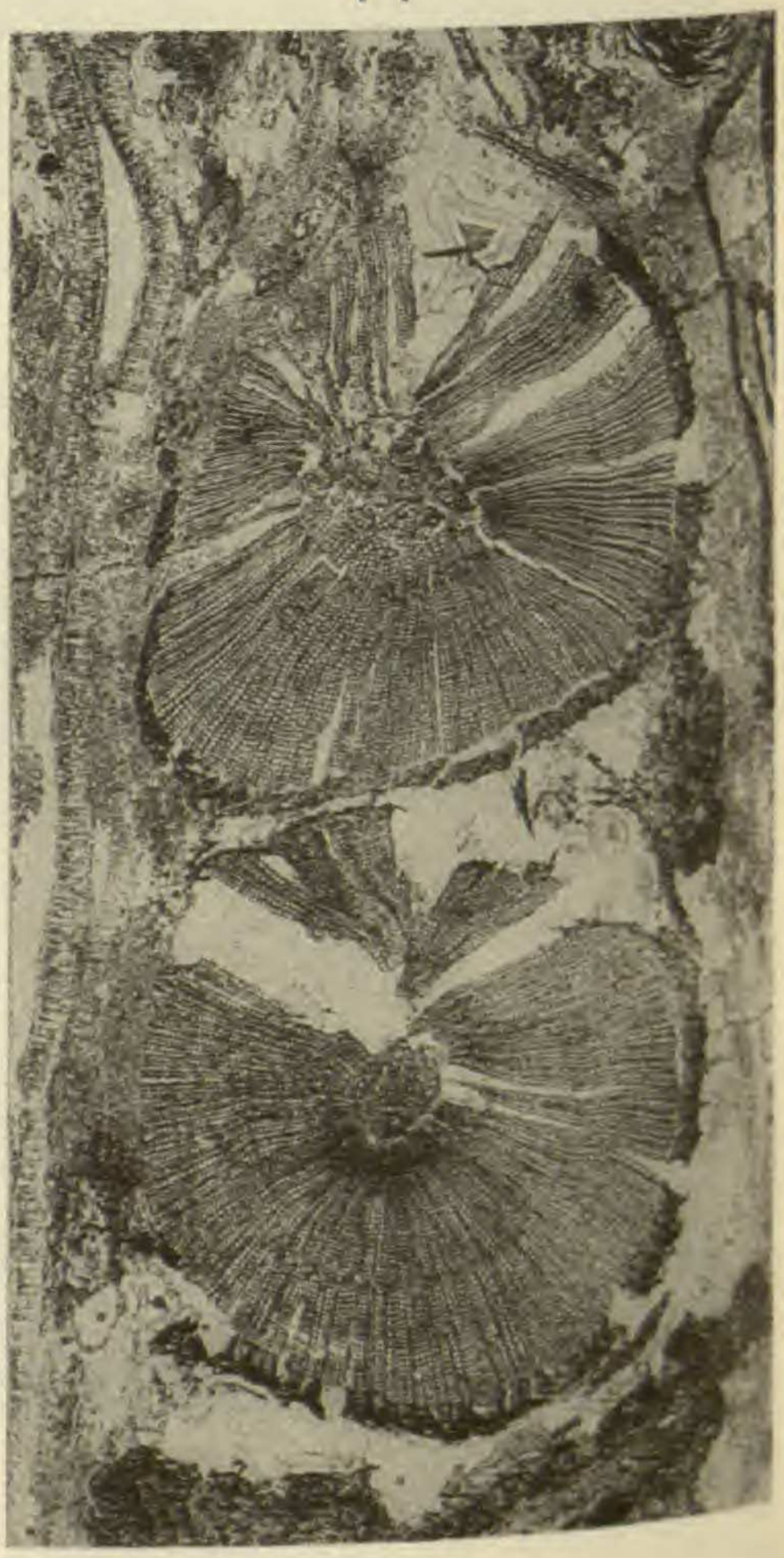


9

10



11



ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

Explanation of Plate

PLATE 20

Fig. 8. *Medullosa grandis.* Transverse section of a small vascular strand, presumably a leaf trace, surrounded by "periderm." Peel 718-B1-t1. × 55.

Fig. 9. *Medullosa distelica.* Transverse section of primary wood. Peel 688-C-b2. × 60.

Fig. 10. *Medullosa distelica.* Transverse section of the outer cortex of the petiole. Peel 688-B-t13. × 25.

Fig. 11. *Medullosa heterostelica* Stewart and Delevoryas. Transverse section showing the two-stelar phase. Peel 819-B-t3. × 2.4.